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Research Article

Dynamic Simulation of Conductance in Apple Tree Canopy

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Abstract: Coupled model of canopy stomatal conductance (G_s) and photosynthesis (P_n) was presented. This model could simulate the response of G_s to microclimatic factors and the diurnal variation. These established models were tested by the observation data in an apple (*Malus domestica* Borkh. cv. 'Fuji') orchard (latitude 40°13' north, longitude 116°13′ east, altitude 79 m). The influences of the microclimatic factors on stomatal conductance were different. There were strong interactions among the various microclimatic factors. From this model, we can see that the diurnal course of G_s in the canopy showed a double-peak curve and G_s increased as the net radiation increased and decreased as the relative humidity and water potential decreased. There was a satisfactory correspondence between measured and simulated values of G_s with observation data in the apple orchard.

Keywords: Apple, diurnal variation, model, stomatal conductance

INTRODUCTION

Both photosynthesis and transpiration rates are regulated by stomatal conductance which depends on environmental factors and plant characteristics including solar radiation, air temperature, relative humidity, air CO_2 concentration, soil and leaf water potential (Damour *et al*., 2010; Naithani *et al*., 2012; Uddling and Wallin, 2012). The simulation models are very important for estimating stomatal conductance. Jarvis (1976) assumed that different environmental variables including solar radiation, air temperature, leaf water potential, vapor pressure deficit, soil moisture deficit and ambient CO_2 concentration acted independently in determining stomatal conductance. Therefore, the model could be expressed in a simple multiplicative form which has been widely used (Damour *et al*., 2010; Egea *et al*., 2011). However, more and more studies showed that stomatal conductance was subject to the feedback of photosynthetic activity (Ball *et al*., 1987; Leuning, 1990). Ball *et al*. (1987) proposed a semi-mechanistic model between stomatal conductance and photosynthesis. Some modified versions of this model were proposed by Collatz *et al*. (1991), Qian *et al*. (2012) and Gao *et al*. (2012). But this model had their defects as they cannot respond to the relationship of main environmental factors. A major challenge is to develop a model which accounts for all the factors which control stomatal conductance.
The aims of our study are:

- Design a coupled model of stomatal conductance which can simulate both the response of stomatal conductance to microclimatic factors and the feedbacks of photosynthesis and transpiration to stomatal conductance.
- Simulate stomatal conductance (G_s) on canopy level in real environment.

Models and methods:
Stomatal conductance model: The model of g_{sc} is given by Leuning (1990):

$$G_{sc} = G_0 + \frac{a_1 A}{(c_s - \Gamma)(1 - D / D_0)} \tag{1}$$

where, a_1, D_0 are constants, D is the vapor pressure deficit and Γ is the CO_2 compensation point. Assuming $G_{sc} = G_s/1.56$, G_s is stomatal conductance for water, modified by the following equation:

$$G_s = 1.56 G_{sc} \cdot G(\Psi_1) \tag{2}$$

where, Ψ_l is leaf water potential which is calculated by Penman-Monteith and water transport model in plant (Gao *et al*., 2010). G (Ψ_l) is a function of Ψ_l (Jones 1992):

$$G(\psi_1) = 1 - \left|\frac{\psi_1}{b_1}\right|^{b_2} \tag{3}$$

where, b_1, b_2 are constants.

Photosynthesis model: The leaf photosynthesis model is based on the mechanistic understanding of C_3

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photosynthesis encapsulated in the description of Farquhar *et al.* (1980) and modified by others (Leuning, 1990; Egea *et al.*, 2011; Qian *et al.*, 2012). The equations describing net photosynthetic rate (A) were given as follows:

$$A = \min\left\{A_c, A_q\right\} - R_d \tag{4}$$

where, A_c is the gross rate of photosynthesis limited by Rubisco activity, A_q is the gross rate of RuBP regeneration through electron transport and R_d is Respiration which is strongly dependent on leaf temperature. If $I = I_{(i)}$ the canopy photosynthesis (P_n) per unit ground area (m^{-2}) is:

$$P_n = \sum_{i=1}^{n} l_i A[I_{(i)}] \tag{5}$$

where, l_i is the leaf area (m^2) of the i^{th} layer (which receives a light intensity $I_{(i)}$ on per unit ground area).

For the biochemical model, the driving variable c_i was calculated according to:

$$c_i = c_a - A/g_{sc} \tag{6}$$

where,
c_a = Air CO_2 concentration
g_{sc} = Stomatal conductance to CO_2

MATERIALS AND METHODS

The experiment was carried out in a 'Fuji' apple (*Malus domestica* Borkh. cv. 'Fuji') orchard from 2013 to 2014. The orchard is in the farm of 'Zhongri' Orchard (latitude 40° 13′ north, longitude 116° 13′ east, altitude 79 m) in Changping county of Beijing. The 'Fuji' apple trees were planted in 1994 in south-north rows at a density of 667 plants/ha. The planting spacing was 5×3 m. Each tree was trained as an open-center system. The soil of the orchard was loam soil and soil water was always adequate.

Leaf stomatal conductance was measured by an AP4 Porometer (AP4, Delta-T, UK). Leaf photosynthetic rate was measured by the Li-6400 Portable Photosynthesis System (LI 6400; LI-COR, USA). The canopy radiant interception was simulated by Beer's law (Johnson *et al.*, 1989). The radiation in different layer of apple tree canopy was measured by LQF5 (Quantum Meter, USA). We presented 3D plots to describe the effects of microclimatic factors and their interaction. All the parameters were estimated with a nonlinear optimization technique or from previous reports (Leuning, 1990; Gao *et al.*, 2010, 2012).

RESULTS

The simulation of canopy stomatal conductance: The response of average G_s of the apple tree canopy (LAI = 3) to the microclimatic factors was presented in Fig. 1. The results showed that G_s were mostly affected by Radiation (R_a) and air Temperature (T_a). G_s increased with the increase of R_a. As T_a increased, the change of G_s followed a bell-shaped curve (Fig. 1A and B). The influence of net Radiation (R_a) on G_s depended on the net radiation flux density. When R_a was below 200 W/m^2, there existed a positive linear relationship between G_s and R_a. G_s did not show a significant increase when R_a increased from 200 to 800 W/m^2 (Fig. 1B and C).

Generally there was a negative correlation between CO_2 concentration and G_s. The effect was stronger when CO_2 concentration was below 350 μmol/mol. However a positive correlation between CO_2 and G_s was found when CO_2 concentration was below 100 μmol/mol (Fig. 1A and C). This was because under low CO_2 concentration the feedback of photosynthesis to G_s was stronger than the effect of CO_2 concentration on G_s. It should be noted that the temperature optimum of G_s shifted to a higher temperature as PAR, CO_2 increased or RH decreased (Fig. 1A, B and D). Strong interactions existed in the various microclimatic factors, especially between T_a and R_a, R_a and CO_2.

Diurnal variation of stomatal conductance: Diurnal changes of G_s of apple trees were simulated by the models (Fig. 2). The microclimatic data used were from June 14th to 19th in 2013 during which it was clear from June 17th to 19th, cloudy from June 14th to 16th. The diurnal course of G_s was simulated according to Eq. (1) and meteorological data. It showed a double-peak type curve on clear days. G_s were at its peaking at mid-morning about 9:30 and mid-afternoon about 15:00. The decline of G_s at noon was caused by RH and Ψ_l. On the cloudy day of 14th to 16th, lower R_a and T_a caused by less sunshine and more clouds led to a decrease in G_s by about 66%, compared to the values on clear days. The change of T_a depended on R_a and had about 2 h lag from R_a. The variation of RH was basically controlled by the variation of T_a since e_a (absolute humidity) remained as a constant. So the radiation intercepted by the canopy became the major factor that affected stomatal conductance in plant. The fluctuation of stomatal conductance was caused by the fluctuation of radiation, too.

The correlations between measured and simulated values of G_s were shown in Fig. 3. For G_s correlation coefficients of the linear regression equations between measured and simulated values was close to 1. The R values for the regressions were also high. Hence, the models and parameters used in this study were good enough to predict G_s with different microclimatic

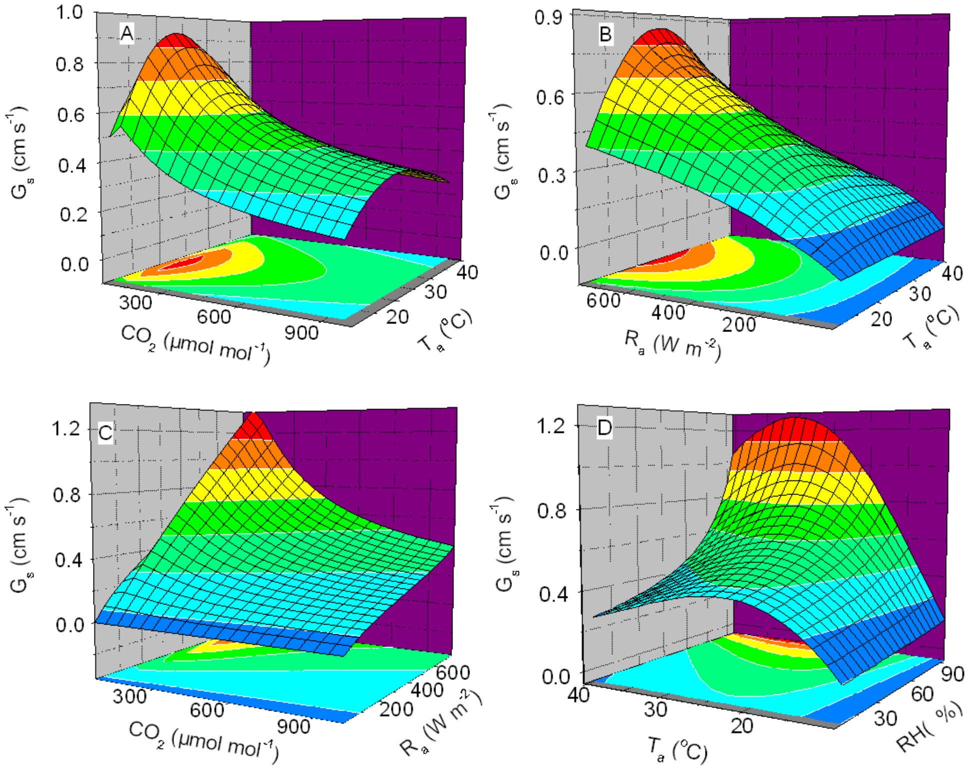

Fig. 1: The response of stomatal conductance (G_s) per unit ground in apple orchard to net radiation flux density (R_a), air relative humidity (RH), air temperature (T_a) and air CO_2 concentration (CO_2)

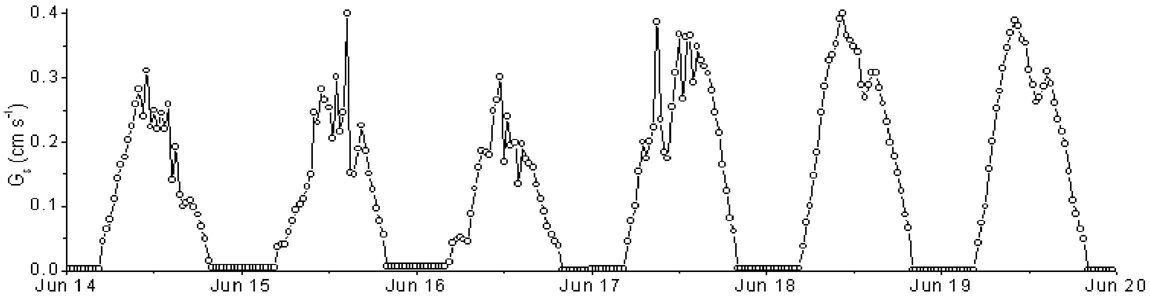

Fig. 2: The diurnal variation of stomatal conductance (G_s) and photosynthesis rate (P_n) per unit ground in apple orchard from June 14th to 19th (LAI = 3)

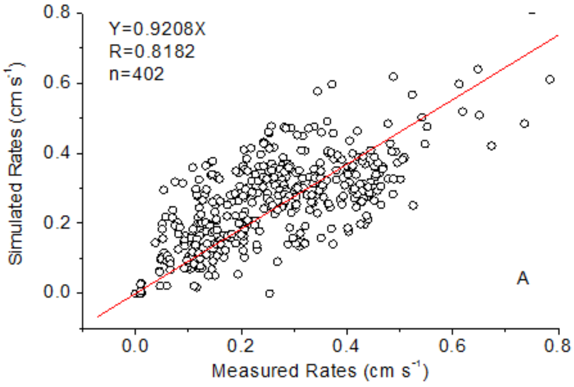

Fig. 3: The relationship between measured and simulated values of stomatal conductance in apple canopy

factors in apple tree canopies. There was a slight underestimation in G_s, which might be caused by light flares and faculae in the canopy.

DISCUSSION

Implementing the coupled models of apple canopy has been successful in predicting the regulation of G_s in response to various microclimatic factors. The models included the feedback of transpiration to stomatal conductance through leaf water potential and the feedback of photosynthesis to stomatal conductance through Ball *et al*. (1987). These models can be applied in the future for solving various theoretical and applied tasks, e.g., the study of plant physiological dynamic, water management in fruit orchards. In addition it can also be used to predict the responses of leaf photosynthetic rates to elevated atmospheric CO_2 concentration and increased temperature, which is fundamental to projecting the impact of global change on the biosphere (Damour *et al*., 2010; Uddling and Wallin, 2012).

The model of stomata is very important for simulating water loss and photosynthetic rates of the plant (Damour *et al*., 2010; Naithani *et al*., 2012; Qian *et al*., 2012). But both the empirical and semi-mechanistic models cannot respond to environmental variables and feedbacks of transpiration and photosynthesis at the same time. Our coupled model solved these problems. The feedback of transpiration to stomatal movement was described with the steady state water flow equation, stomatal model and P-M equation. And through semi-mechanistic model of stomatal conductance and biochemical model of photosynthesis the feedback of P_n to stomatal behavior was described. Leaf water potential might have acted as a hydraulic signal to partly closing stomata (Shahnazari *et al*., 2007). Then the connection between T_r and P_n was established through the stomatal model. There were strong interactions between the various microclimatic factors. Therefore, we should consider the interactions when discussing the influences of environmental factors on stomatal conductance. In our study the maximum G_s occurred at air CO_2 concentration of 100 μmol/mol because of the feedback of P_n. This result is similar to other studies (Dubbe *et al*., 1978).

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